OBSERVATIONS ON THE EPIDERMAL STRUCTURE AND STOMATAL APPARATUS OF SOME MEMBERS OF THE ARACEAE

EDGAR E. WEBBER[1]

Engler (4) determined that if the *Araceae* were to be classified as a natural group, flower structure alone was insufficient. Detailed anatomical and morphological study led him to classify the family into eight subfamilies, the Pothoideae, Monsteroideae, Calloideae, Philodendroideae, Lasioideae, Colocasioideae, Aroideae, and Pistioideae.

An earlier taxonomic work by Engler was published by DeCandolle (3) and was basically similar to his aforementioned system, except that in his earlier study Engler had *Calla* placed with the Pothoideae, *Nephthytis* and *Syngonium* included in the Lasioideae, and *Dieffenbachia* and *Aglaonema* were separated out into the Aglaonemoideae. The later study caused Engler (4) to include *Calla* in the Calloideae, a new subfamily; *Syngonium* was removed to the Colocasioideae, and *Dieffenbachia* and *Aglaonema* were placed in separate tribes in the Philodendroideae.

Following this more complete system, then, representatives of all but two subfamilies, the Calloideae and Pistioideae, were studied. Members of these two groups were unavailable for my work.

MATERIALS AND METHODS

Mature leaves were taken from plants grown under similar environmental conditions in a greenhouse and cut into sections approximately 4 mm. square. These were immediately fixed in formalin-propionic-acid, then embedded in paraffin, sectioned, and stained with safranin and fast green. Cross sections were made at 10μ, and paradermal sections at 12 to 14μ. No distinction was made in the cross sections as to whether they were parallel with or at right angles to the main axis of the leaf.

DISCUSSION AND RESULTS

A. EPIDERMIS. — Dalitzsch (2) noted that the epidermal

[1]I wish to thank Dr. F. M. Hueber for making the drawings (Fig. 1-8) from my photomicrographs.

cells found in various genera of the *Araceae* were of different sizes and shapes. Also, that in *Amorphophallus bulbifer*, *Homalomena coerulescens*, and *Alocasia cuprea* undulations of the side walls occurred, as seen in surface view. He made no distinction as to which epidermis was concerned. Of the genera sampled in this study the following situations were observed. In *Nephthytis Cravenreuthii* both epidermal layers have cells with most pronounced side wall undulations (Fig. 1). *Aglaonema costatum*, *A. pictum*, and *A. marantaefolium* show undulated walls only in upper epidermal cells. *Crytosperma Johnstonii* shows the undulations, not as pronounced, present in both epidermal layers. The lower epidermis of *Arisarum vulgare* and the upper epidermis of both *Arum italicum* and *Arum hygrophyllum* exhibit very weakly undulated cell walls. Watson (7) proposes an explanation of waviness of epidermal cell walls on the method of hardening of the differentiating cuticle. Working with *Hedera helix* L., he determined that most undulations appeared in leaves grown in light shade.

In cross sectional aspect the epidermal cells may be raised in their centers giving the entire cell a more or less dome shaped appearance. Such was observed in *Porphyrospatha Hoffmannii*, *Philodendron gloriosum*, *Philodendron andreanum*, and *Scindapsus pictus argyreus*. *Anthurium crystallinum* and *Spathiphyllum floribundum* are also of this nature. Dalitzsch (2) reported a button-like papilla in *Colocasia antiquorum* which may be an extreme development of the phenomenon reported here (Fig. 2). In addition the aforementioned *Porphyrospatha* has the outer walls of the lower epidermal cells rounded. Some genera show more raising of the epidermal cells than others.

The cuticle of several species exhibited various degrees of "ribbing" which may occur on either epidermis or on both. In surface view the "ribs" may be in the form of roughly parallel striations (Fig. 3), or may be arranged in a complex pattern (Fig. 4). Plants with cuticles of the former type include *Prophyrospatha Hoffmannii*, *Pothos hermaphroditus*, *Pothos jambea*, *Aglaonema costatum*, *Aglaonema pictum*, *Aglaonema marantaefolium*, *Homalomena pygmea*, and *Spathiphyllum cannaefolium*.

FIG. 1

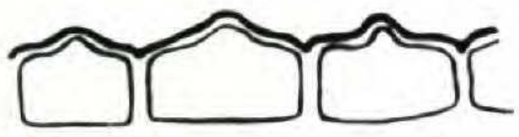

FIG. 2
(After Dalitzsch)

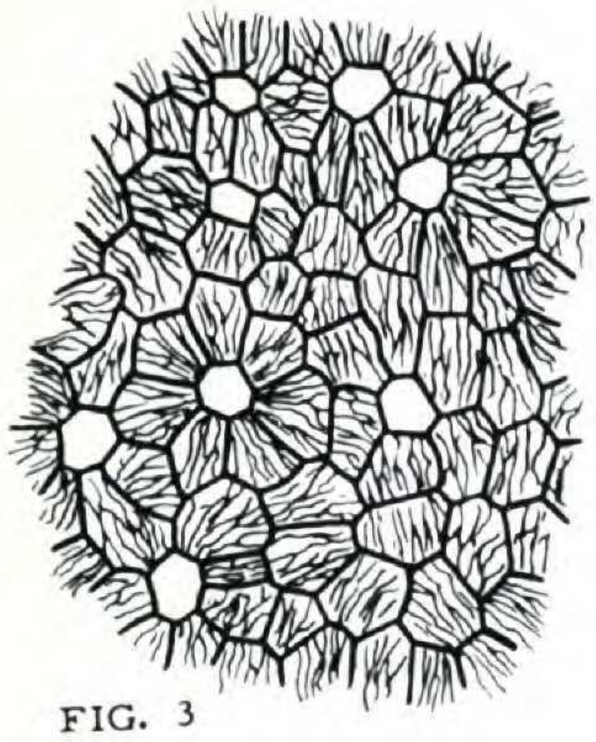

FIG. 3

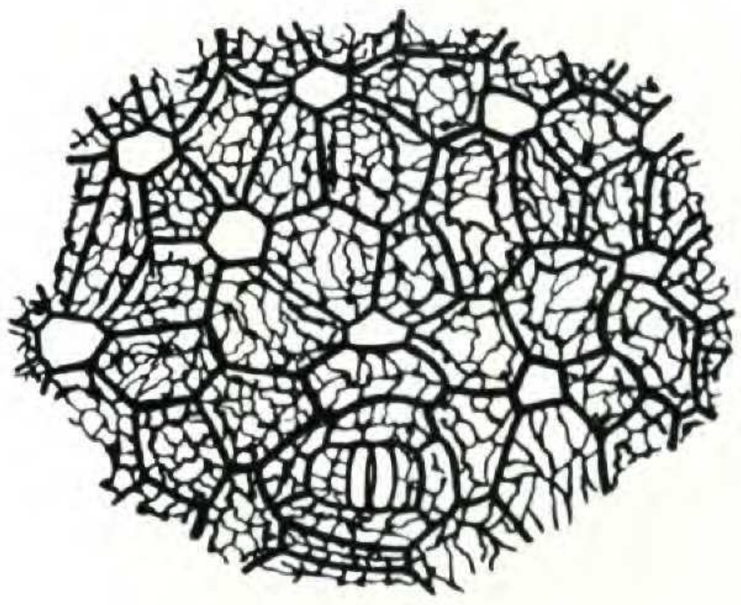

FIG. 4

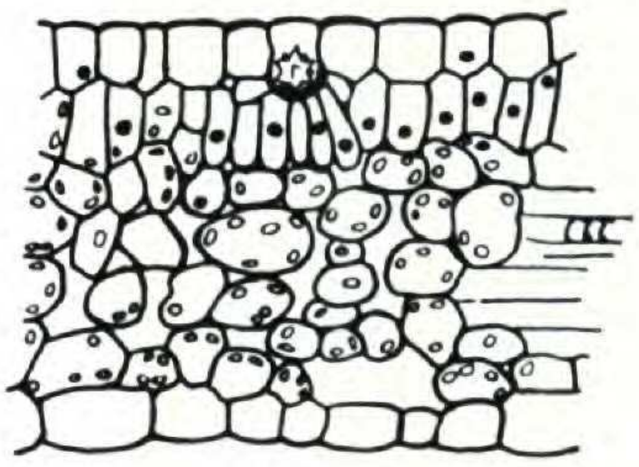

FIG. 5a

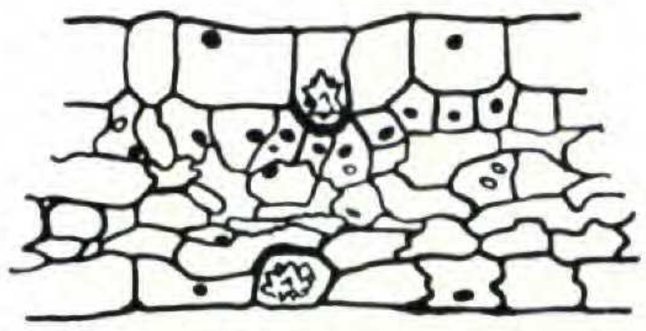

FIG. 5b

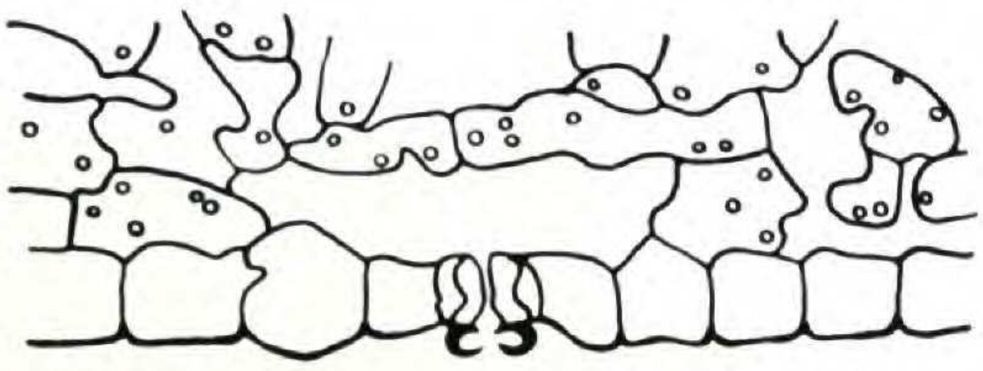

FIG. 6

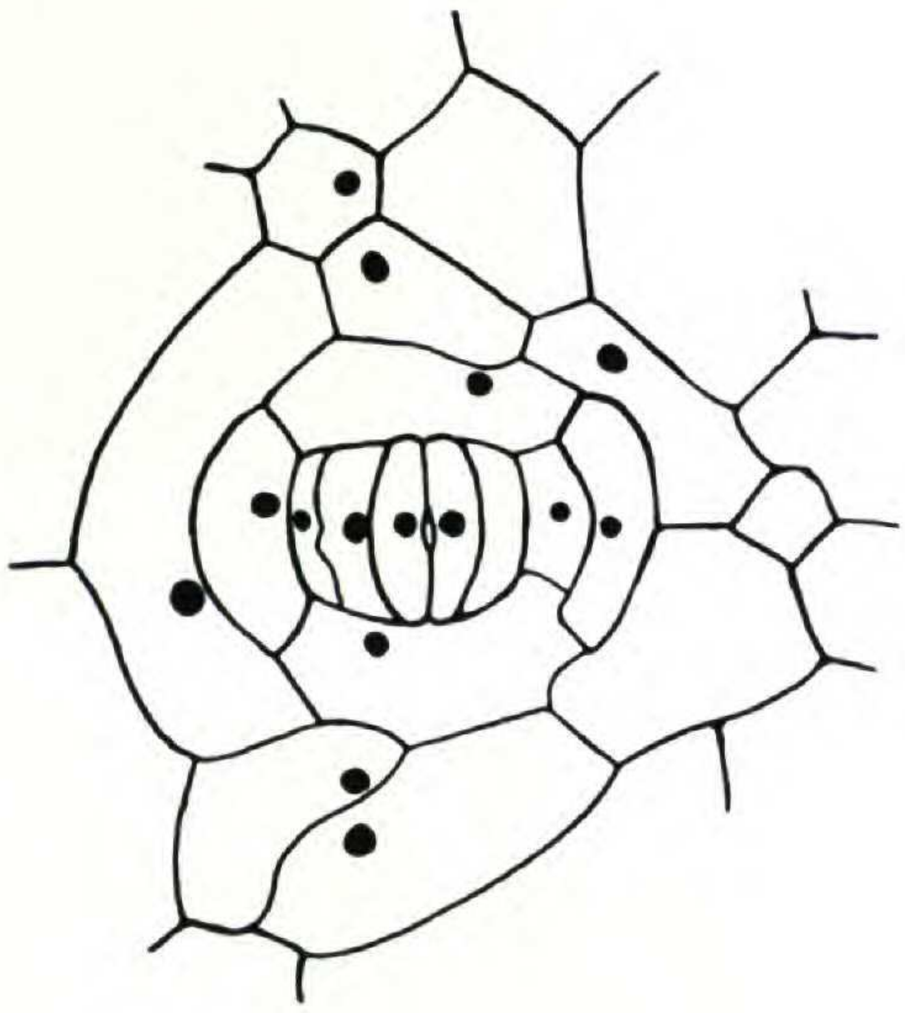

FIG. 8

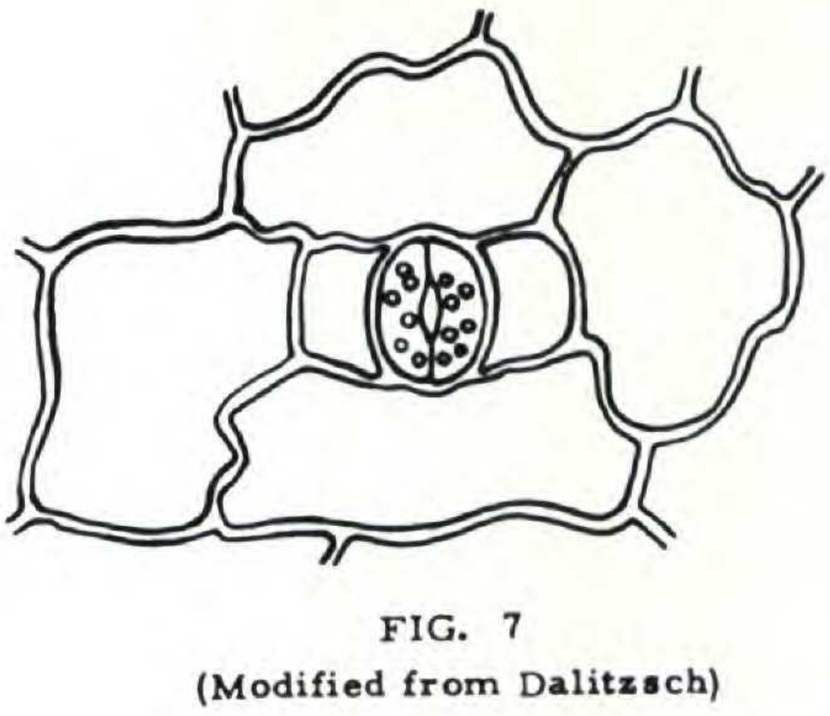

FIG. 7
(Modified from Dalitzsch)

An interesting feature was noted in the epidermis of the two species of *Pothos*. In surface view the epidermal cells radiate like spokes in a wheel from a central, somewhat circular cell. Under oil it was observed that this central cell appeared to have depth due to wall thickenings which became evident upon focusing at different levels. An examination of cross sections showed these thickenings to be due to the cell walls of certain palisade cells which orient themselves beneath the epidermal cell (Fig. 5a). In *Pothos jambea* a crystal is invariably present in such an epidermal cell (Fig. 5b). With polarized light it was noted that the radiating arms of these crystals, as seen most clearly in *Pothos hermaphroditus*, assume the form of an arrowhead.

Dalitzsch (2) mentioned that in the lower epidermal cells of *Anthurium Scherzerianum* and *A. magnificum* the occurrence of calcium oxylate granules, and these he called "druzen". Of the species considered here only *Anthurium scandens* was found to contain such cells. These "druzen" can be observed macroscopically as small, dark dots in the under surface of the leaf. Microscopic sections failed to give clear and definite evidence for the presence of such cells, and accordingly free-hand sections of several leaves were made. Here it was noted quite clearly that the "druzen" was not a cell but an aggregation of cells, differing in appearance from the epidermal cells, circularly arranged about what appeared to be a central pore. The exact nature of this pore was not determined, nor did it seem in any way like a stoma. Furthermore, each cell in this ring, and the number of rings of cells varied from one to three, was completely filled with a dark brown substance. Dalitzsch (2) had also applied the term "druzen" to an extracellular substance which collected under the epidermis.

Many genera in the *Araceae* have perforations of varying sizes in their leaves. In *Monstera deliciosa*, for example, the exact cause of these holes is unknown. By examination of the leaves of *Epipremnum pinnatum* the sequence in their formation was clearly seen. First, a small, non-chlorophyllous dot appeared. This enlarged slightly, followed by the presence of a tiny hole in the center of this white dot.

Through an increase in size this hole soon appeared as the typical perforation. The latter varied in size not only from leaf to leaf but also in the same leaf.

B. STOMATA. — In cross section, the accessory cells were seen to partially surround the guard cells, and the wall of the latter which was farthest from the stomatal pore was slightly concavely bent. This was true in all plants studied. The stomata neither extended above nor below the epidermal surface. Wall thickenings of the guard cells gave the appearance of "horns" in all species. The length of these horns was not constant, but varied with the specimen from very short protuberances to rather long and reflexed ones. *Schismatoglottis* and *Arisarum* are examples of the former, while the latter was seen in *Aglaonema marantaefolium* (Fig. 6).

With respect to the type of stomatal apparatus, Dalitzsch (2) distinguished two types "from which one species or another deviates only in a small degree". In surface view one kind of apparatus is seen to consist of one pair of accessory cells at the sides of the guard cells (Fig. 7). The second general type has two pairs of accessory cells at the sides and one additional pair which limit the top and bottom of the stoma, giving the appearance of a ring of four cells about the stomate, thus showing a total of six accessory cells (Fig. 4). In *Pothos jambea* this ring often has an additional accessory cell at the side, giving a total of seven or eight (Fig. 8). The upper epidermis of *Philodendron bipanifolia* has two pairs of accessory cells at the sides of the guard cells, and only occasionally is there a full ring present. The upper epidermis of *Monstera deliciosa* also exhibited a diversion from the one ring type; here, the first pair of accessory cells often appeared as two individual cells occupying the space where normally one accessory cell would be. This two-celled condition may be either on one or on both sides of the guard cells. Another variation noted by Dalitzsch (2) in *Dieffenbachia Seguine* was the occurrence of a double or triple ring of accessory cells. In *Dieffenbachia Hoffmanii* great variation in the type of stomatal apparatus was manifested, and in a few cases such a double ring was seen. *Monstera deli-*

TABLE I. Plants listed according to type and distribution of stomatal apparatus[1].

I.

a) *One pair of accessory cells*
Nephthytis Cravenreuthii
Philodendron gloriosum
Philodendron Florida compacta
Philodendron andreanum
Anthurium undatum
Anthurium scandens
Anthurium crystallinum
Aglaonema pictum

b) *One ring of four accessory cells*
Scindapsus aureus
Philodendron lacineatum
Spathiphyllum floribundum
Pothos jambea

II.

Syngonium erythrophyllum
Prophyrospatha Hoffmannii
Monstera acuminata
Monstera sp.
Dieffenbachia Hoffmannii
Philodendron auriculatum
Spathiphyllum cannaefolium

III.

a) *One pair of accessory cells*
Epipremnum sp.
Spathicarpa sagittifolia
Arisarum vulgare
Arum italicum
Arum hygrophyllum

III.

b) *One ring of four accessory cells*
Monstera Friedrichsthalii
Schismatoglottis nova-guineensis

IV.

a) *Upper epidermis one pair of accessory cells; lower, one ring of four*
Philodendron oxycardium
Rhodospatha picta

b) *Upper epidermis with two lateral pairs of accessory cells; lower, one ring of four*
Philodendron bipanifolia

c) *Upper epidermis poorly preserved; lower with one ring of four*
Scindapsus pictus argyreus
Epipremnopsis Huegueliana

V.

Philodendron cordatum varigatum
Syngonium podophyllum
Pothos hermaphroditus
Crytosperma Johnstonii
Aglaonema costatum
Homalomena pygmea
Epipremnum pinnatum
Monstera deliciosa

VI.

Raphidophora celatocaulis

[1]I - Stoma on lower epidermis only; same apparatus.
II - Stoma on lower epidermis only; apparatus variable.
III - Stoma both surfaces; apparatus same for a given layer or for both layers.
IV - Stoma both surfaces; apparatus different.
V - Stoma both surfaces; apparatus similarly variable.
VI - Stoma both surfaces; lower epidermis constant, upper variable.

ciosa, in addition to the above phenomenon, often appeared to approach the double ring condition, but it was difficult to determine whether this might in part be due to flattened epidermal cells rather than distinct accessory cells. *Syngonium podophyllum* and *Pothos hermaphroditus* also appeared to approach the double ring condition.

Contrary to earlier work (2), the *Araceae* can not be separated into two groups each based on a distinct type of stomatal apparatus, for the following situations are evident: an epidermis may be entirely of one type of apparatus; an epidermis may vary in the type of apparatus; two epidermal layers may be of one type, or they both may have a similar variation in the type of apparatus; one epidermis may vary in one type while the other is constant for a different type; or, both epidermal layers may be of the same type of apparatus.

Table I summarizes the species studied as to their stomatal apparatus.

CONCLUSIONS

It is customary to consider variability to be a primitive characteristic and constancy to be advanced. The Pothoideae would then be expected to show, perhaps, the most variation in stomatal apparatus, if the latter were to be used as a taxonomic feature. Bailey and Nast (1) found that stomatal features were of value in the anatomy and taxonomy of the *Winteraceae*. Rea (6) has also shown that the number of stomates in *Campanula* increases with light and dry habitat. Florin found the stomatal apparatus to be of very great significance in the taxonomy of the Cycads and Cycadeoides.

While anatomical details of the *Araceae* have here been further expanded and elaborated, it is doubtful if any taxonomic significance can be drawn from these findings.

Literature Cited

1. Bailey, I. W., and C. G. Nast. The Comparative Morphology of the *Winteraceae*, V. Foliar Epidermis and Sclerenchyma. Jour. Arnold Arb. **25**: 342-348. 1944.
2. Dalitzsch, M. Beiträge zur Kenntniss der Blattanatomie der Aroideen. Botanisches Centralblatt. 25. 26. 1886.
3. DeCandolle, A. and C. Monographiae Phanerogamarum. 2. Sept. 1879.

4. ENGLER, A. Das Pflanzenreich. Heft 74: 63-66. Araceae pars generalis et index familiae generalis. Leipzig. 1920. Facs. ed. 1957.
5. ESAU, K. Plant Anatomy. New York. 1953.
6. REA, M. Stomata and Hydathodes in *Campanula rotundifolia* L., and their Relation to Environment. New Phytol. **20**: 56-72. 1921.
7. WATSON, R. W. The Effect of Cuticular Hardening on the Form of Epidermal Cells. New Phytol. **41**: 223-228. 1942.

STEPPE, TAIGA, AND TUNDRA.[1] — Anyone here-abouts contemplating "the magnificent Flora USSR" may have wondered: "But what if some regional botanist within its range should desire to publish a flora of his area? Would that be allowed, and would divergent views in systematic botany be permitted, let alone supported, by national science organizations in the USSR?" That the answer is "yes" is signified by the appearance and contents of this two volume Flora of Central Siberia, by M. G. Popov. In addition to this, floras of the Murmansk, Tadzhik, Caucasus, Yakut, and Northern Mongolia regions have appeared during the 1950's.

The territory covered by this flora, as defined by the author, is 2000 kilometers east to west, and 1000 kilometers north to south. Westward its limit is 92° east longitude in the Enisee area, and eastward it extends to 122° east l., or the Olekmoi line; northward to the 60th parallel, and southward to about the 48th parallel, or the border of the Mongolian Peoples' Republic. A glance at a map of Canada will show that Alberta, Saskatchewan, and Manitoba, with southeastern British Columbia east of 120°, form a block almost exactly the same size, occupying almost the same territory latitudinally and longitudinally in the western hemisphere. In both territories the drainage is northeastern and northwestern, and within them eastern and western floristic elements of their respective continents meet.

The author, Popov, defines therein 6 principal areas: 1. The Eniseian; 2. The Saian Mountain Taigan area, mountains with a rich alpine flora, and a pine — larch taiga; 3. The Central Siberian Taigan area, mostly high plateau, with

[1]The Flora of Central Siberia by Mikhail Grigorevich Popov. Vol. I, 1957. pp. 1-556. Pls. 1-65. Vol. II, 1959. pp. 557-920. Pls. 66-104. Published by the East Siberian Affiliate of the USSR Academy of Sciences, Moskow — Leningrad. Foreword by Boris K. Shishkin, editor. Price approximately $4.00 per volume in US currency.